Evolution of sexual size dimorphism in grouse and allies (Aves: Phasianidae) in relation to mating competition, fecundity demands and resource division

T. LISLEVAND,* J. FIGUEROLA† & T. SZÉKELY‡

*Bergen Museum, The Natural History Collections, University of Bergen, Bergen, Norway
†Department of Wetland Ecology, Estación Biológica, Doñana, Sevilla, Spain
‡Department of Biology and Biochemistry, University of Bath, Bath, UK

Abstract

Sexual size dimorphism (SSD) is often assumed to be driven by three major selective processes: (1) sexual selection influencing male size and thus mating success, (2) fecundity selection acting on females and (3) inter-sexual resource division favouring different size in males and females to reduce competition for resources. Sexual selection should be particularly strong in species that exhibit lek polygyny, since male mating success is highly skewed in such species. We investigated whether these three selective processes are related to SSD evolution in grouse and allies (Phasianidae). Male-biased SSD increased with body size (Rensch's rule) and lekking species exhibited more male-biased SSD than nonlekking ones. Directional phylogenetic analyses indicated that lekking evolved before SSD, but conclusions were highly dependent on the body size traits and chosen model values. There was no relationship between SSD and male display agility, nor did resource division influence SSD. Although clutch mass increased with female body size it was not related to the degree of SSD. Taken together, the results are most consistent with the hypothesis that lekking behaviour led to the evolution of male-biased SSD in Phasianidae.

Introduction

In most mammals and birds males are larger than females, whereas among invertebrates and fishes females tend to be the larger sex (Darwin, 1871; Andersson, 1994; Fairbairn *et al.*, 2007). Although this variation in sexual size dimorphism (SSD) has received considerable attention among evolutionary biologists for over a century, neither the adaptive function nor the genetic/developmental bases of SSD are fully understood. Comprehensive tests of functional hypotheses on SSD evolution are thus needed to understand why and how SSD has emerged, and is being maintained in contemporary populations (Fairbairn, 2007; Székely

et al., 2007). Numerous explanations of SSD exist, predicting differential strength and/or direction of selection pressures acting on male and female body sizes (reviewed by Shine, 1989; Andersson, 1994; Blanckenhorn, 2005; Fairbairn *et al.*, 2007). Here we focus on three major hypotheses.

Firstly, directional selection towards large males is expected when male body size favours mating success, either because females prefer to mate with larger males, or because larger males are more successful in monopolizing territories or breeding resources in male-male contests (Andersson, 1994). Also, many animal groups show an allometric relationship between male and female body size where SSD increases with body size among species when males are larger than females, but decreases when females are larger ('Rensch's rule'; Fairbairn, 1997). In birds, sexual selection is driving this allometric relationship (Székely *et al.*, 2004; Dale *et al.*, 2007). Mating system is often used as a proxy for the

Correspondence: Terje Lislevand, Bergen Museum, The Natural History Collections, University of Bergen, PO Box 7800, 5020 Bergen, Norway.
Tel.: (+47) 55 58 29 07; fax: (+47) 55 58 96 77;
e-mail: terje.lislevand@bm.uib.no

intensity of sexual selection, because in polygynous mating systems the mating success is often skewed (Lack, 1968; Webster, 1992; Owens & Hartley, 1998; Székely et al., 2000; Dunn et al., 2001). The strongest sexual selection is expected in species in which males gather on mating arenas, or leks, to compete for females. Such lekking species are also characterized by female-only care and a highly skewed mating success (Höglund & Alatalo, 1995). However, comparative analyses of lekking and SSD have produced controversial results, and the importance of lekking in promoting SSD is debated (Höglund, 1989; Oakes, 1992; Höglund & Sillén-Tullberg, 1994). It is possible that sexual selection favours small male size in species of which the males display acrobatic flights in the air (Andersson & Norberg, 1981; Jehl & Murray, 1986; Mueller, 1990; Figuerola, 1999; Székely et al., 2004; Raihani et al., 2006). Small body size enhances manoeuvrability by making males more agile and better able to perform in flight acrobatics.

Secondly, egg size and clutch mass often increase with female body size both in fishes and birds (Berglund et al., 1986; Christians, 2002), and chicks hatching from large eggs are often more viable than those hatching from small ones (Williams, 1994; Blomqvist et al., 1997). Consequently, demands of egg production may favour increases in female body size (the fecundity hypothesis). A female bird's total egg investment may be reflected by the total clutch mass, hence depending both on the number and size of eggs that are produced per clutch. Therefore we predict that clutch mass, female size and female size relative to male body size should be positively correlated (Darwin, 1871; Reeve & Fairbairn, 1999).

Thirdly, SSD may evolve as a response to competition for resources between males and females, making the sexes able to utilize different ecological niches (the resource division hypothesis; Selander, 1966; Shine, 1989; Temeles & Kress, 2003). Accordingly, we predict SSD to increase with the proportion of time the two sexes need to share resources available in a given location, e.g. a territory (Székely et al., 2007).

Using comparative methods we tested these major hypotheses of SSD evolution in grouse and allies (Phasianidae, 176 species; Monroe & Sibley, 1993). This avian family is distributed across Eurasia, Africa and North-America, and shows some of the largest range of SSD in any bird group (Székely et al., 2007). The Phasianidae also exhibit a range of breeding systems from social monogamy to lek polygyny, and there is variation across species in pair bond duration, territoriality and gregariousness. Clutch sizes vary from one or two eggs to over 15 eggs per clutch (Madge & McGowan, 2002). Hence, the Phasianidae are well suited for comparative analyses of SSD.

A number of studies have previously addressed SSD in grouse and allies (Wiley, 1974; Sigurjónsdóttir, 1981; Sæther & Andersen, 1988; Höglund, 1989; Oakes, 1992; Höglund & Sillén-Tullberg, 1994; Drovetski et al., 2006;

Kolm et al., 2007). Our work is distinct from these studies for three important reasons. First, we use the most comprehensive dataset to date by incorporating species spanning the whole family. This increases statistical power and provides results that are relevant to the whole family. Secondly, to take phylogenetic effects into account, we use Generalized Least Squares (GLS). This is an advanced phylogenetic method (Pagel, 1997, 1999; see also Kolm et al., 2007) that makes less restrictive assumptions on models of trait evolution than previous methods. Thirdly, we use directional phylogenetic analyses for the first time to test the temporal appearance of SSD relative to lekking behaviour. In addition, Rensch's rule was previously supported in the Phasianidae, based on analyses of restricted datasets (Sæther & Andersen, 1988; Fairbairn, 1997; Drovetski et al., 2006). Low sample sizes may affect the conclusions of such analyses (Székely et al., 2004; Lindenfors & Tullberg, 2006). We therefore also include a comprehensive test of Rensch's rule across the whole family.

Methods

Dataset

We collated data from the literature on body mass (g) and wing length (mm) separately for adult males and females, egg mass (g) and clutch size, as well as verbal descriptions of social mating system, male sexual display behaviour and inter-sexual resource sharing (see definitions and justification in Lislevand et al., 2007). Appendix 1 shows data and literature references. As far as possible we restricted body mass data to measurements taken during the breeding season. Wing lengths were taken from stretched and flattened wings, and egg masses refer to fresh eggs. Mean values of body mass, wing length and clutch size were preferred, but if these were not available we calculated the mid-points of reported ranges instead. Species in which less than three individuals were measured for a given sex were excluded from analyses. When data were available from more than one source, we used the one with the largest sample size. Body mass, wing length, clutch size and egg size were log_{10}-transformed before the analyses. SSD was calculated as log_{10} (male size) $- log_{10}$ (female size); see Fairbairn (2007) for rationale.

Mating system, sexual display type and resource sharing were scored according to predefined categories (see also Figuerola, 1999; Raihani et al., 2006; Székely et al., 2007). Mating system was dichotomized as (1) nonlekking (monogamy or resource-defence polygyny) or (2) lek polygyny. These scores were taken as indicative of the intensity of mating competition. Males may court or fight on ground, or exhibit displays that include jumping into the air. Displays were thus scored as (1) ground display, including display on trees and on bushes, (2) ground display, but with occasional leaps and jumps

into the air and (3) both ground and aerial displays including jumps. Note that these scores correspond to a scoring scheme we have used for birds in general (Lislevand *et al.*, 2007; Székely *et al.*, 2007), although in grouse no species exhibited acrobatic displays (scores 4 and 5 in Lislevand *et al.*, 2007).

We used the extent of temporal resource sharing between members of a 'pair' as a proxy for resource division: (1) males and females do not share resources, and feed away from their breeding site, (2) males and females share resources on their territory only during the breeding season and (3) males and females share resources on their territory all year round. As the resource division hypothesis does not predict which sex should be largest, we use the absolute values of SSD.

For both sexual display and resource sharing we collated descriptions from primary literature and reference books (see Appendix 1), and scored these verbal descriptions according to our definitions (see above). Scoring was carried out independently by three observers, blindly to species identity. Scores were highly consistent among the observers (display agility: $r_S = 0.87 - 0.90$; resource sharing: $r_S = 0.46 - 0.60$). For those scores that were different between observers, we took the median score. If one (or more) observer was unable to score a description, this datum was excluded from the analyses.

Phylogeny

We constructed a composite phylogeny from phylogenetic studies of Phasianidae based on mitochondrial sequences (Fig. 1). Relationships between genera were taken from Kimball *et al.* (2001) and within the Tetraoninae from Dimcheff *et al.* (2002). Within-genera topologies were taken from Randi & Lucchini (1998) for Alectoris, Kimball *et al.* (1999) for Gallus, Bloomer & Crowe (1998) for Francolinus and Moulin *et al.* (2003) and Hennache *et al.* (2003) for Lophura. In all phylogenetic analyses branch lengths were set to unity. We carried out analyses assuming polyphyly or monophyly of the genus Francolinus and by using each species as an independent datum. We only report results of the former analyses, unless there were qualitative differences among the three sets of analyses.

Analyses

The relationships between SSD and explanatory variables was tested using CONTINUOUS (Pagel, 1997, 1999), based on GLS models to test for correlated evolution between two characters. First, we estimated the parameter λ by maximum-likelihood. The λ parameter estimates the degree of phylogenetic influence on trait covariance. The case of $\lambda = 0$ corresponds to characters
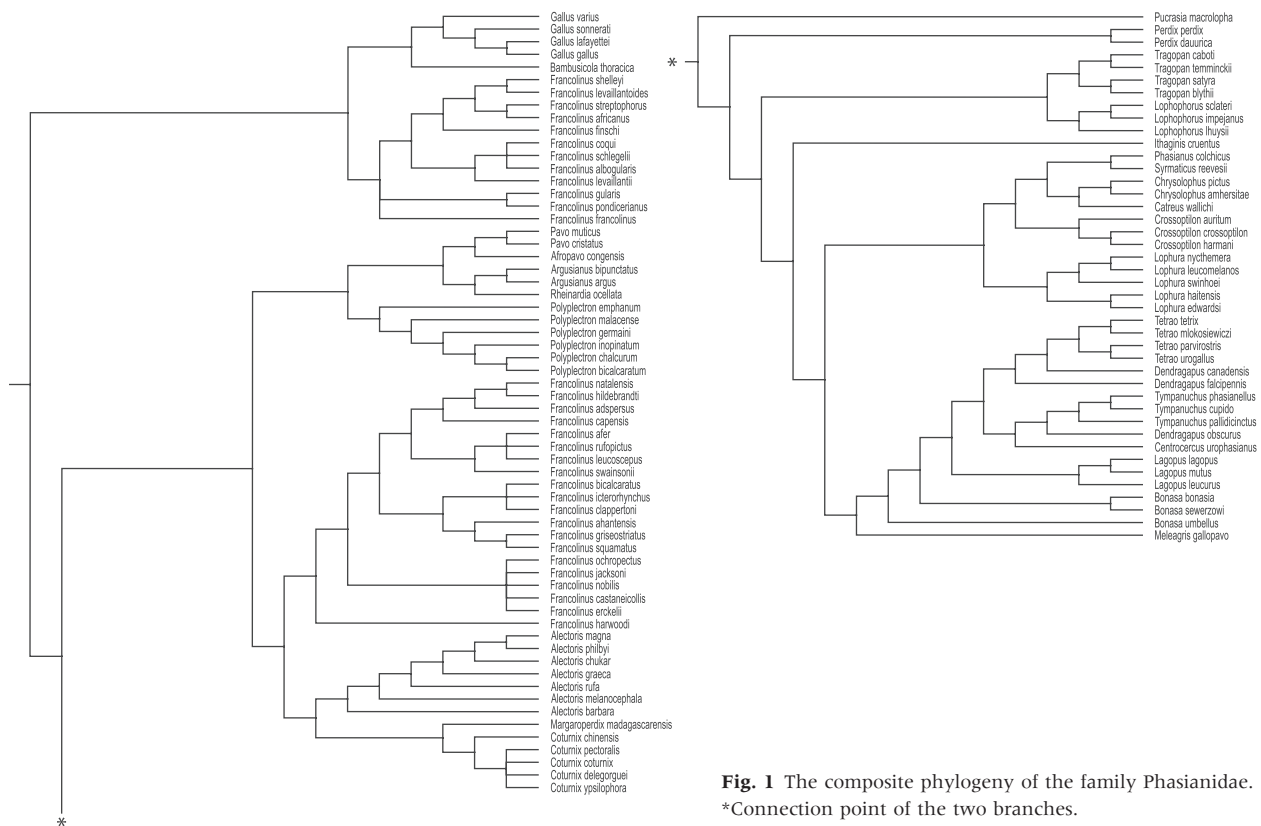

Fig. 1 The composite phylogeny of the family Phasianidae. *Connection point of the two branches.

evolving independently from the phylogeny, and $\lambda = 1$ indicates Brownian motion of evolution (Pagel, 1999). Secondly, using the estimated λ, the correlation between pairs of traits was tested by log-likelihood ratio (LR) test by comparing the model forcing the correlation to be zero, with the alternative model allowing correlated evolution between the two characters. For each analysis we present the estimated scaling parameter and the log-LR test for correlated trait evolution. When controlling for potentially confounding factors, we entered these variables together with the variables of interest in the same model, and tested for correlated trait evolution. If the model offering the best fit with the data allowed correlation among traits, we calculated the partial phylogenetic correlation for each independent variable in the model.

To analyse directional evolution of SSD in relation to mating competition (lekking vs. nonlekking), we created binary traits of SSD using several alternative categories. A species was said to show male-biased SSD if (1) males were on average > 10% heavier than females or had > 5% longer wings (Höglund, 1989), or male-biased SSD was larger than (2) the mean, (3) median or 4) midpoint of SSD across species. We used DISCRETE (Pagel, 1994, 1997) for these analyses. This program is based on a Markov model for trait evolution and allows for investigation of correlated evolution between two binary traits and test the directionality and temporal order of change in two discrete traits. The statistical significance of differences between the evolution-dependent and -independent models was determined using Monte Carlo simulations because the statistic does not match any commonly used statistical distribution. The LR obtained from the data was compared with those derived from 1000 runs simulating the evolution of the two characters studied over the phylogeny using the independent model parameters. The directionality of the significant relationships was tested according to Pagel (1994), by forcing the two parameters in the model of dependent evolution coding for trait transitions in one or the other direction to take the same value. For example, to determine whether large male-biased SSD is associated with the evolution of a lek mating system, the probabilities of change in mating system in species with large and small SSD were forced to take the same value. If this model had a significantly reduced fit to the data, the hypothesis of equal probability of change with respect to SSD was rejected. In these analyses, statistical significance of the changes in likelihood was determined using the chi-square distribution (1 d.f.). Pagel's method cannot deal with polytomies (multiple speciation events or unresolved parts of the tree; see Fig. 1), so for the DISCRETE analyses a fully resolved parsimonious version of the phylogeny was used (i.e. the tree minimizing the number of evolutionary changes in the characters of interest).

We test Rensch's rule by entering logarithms of male and female body size into a major-axis regression, placing male size on the y-axis (Fairbairn, 1997). Rensch's rule is supported if the slope β of the resulting regression line is > 1. We tested this by estimating 95% confidence intervals (CI) for slopes using R (R Development Core Team, http://www.R-project.org). We calculated phylogenetically independent contrasts of male and female body sizes using comparative analysis by independent contrasts (CAIC) (Purvis & Rambaut, 1995). The body mass data violated the assumption that absolute values of contrasts are independent of their standard deviations (Garland *et al.*, 1992), and we therefore only test for Rensch's rule in wing length contrasts. Contrasts were analysed using a major-axis regression forced through the origin. Note that we use phylogenetically independent contrasts instead of performing GLS regressions on species data, because we are not aware of any ways to perform major-axis regressions using GLS.

Results

Distribution of SSD and Rensch's rule

On average, male phasianids were larger than females in both traits (Wilcoxon-matched pairs tests, body mass: $Z = -6.98$, $P < 0.001$, $n = 73$ species; wing length: $Z = 8.06$, $P < 0.001$, $n = 93$ species; Fig. 2). There were only eight of 73 species and seven of 93 species in which females were larger than males in body mass and wing length respectively.

Rensch's rule was strongly supported at species-level analyses (body mass: $\beta = 1.145$, 95% CI = 1.061–1.237, $n = 73$; wing length: $\beta = 1.146$, 95% CI = 1.103–1.191, $n = 93$) and using phylogenetically independent contrasts (wing length: $\beta = 1.110$, 95% CI = 1.011–1.223, $n = 84$ contrasts; Fig. 3).
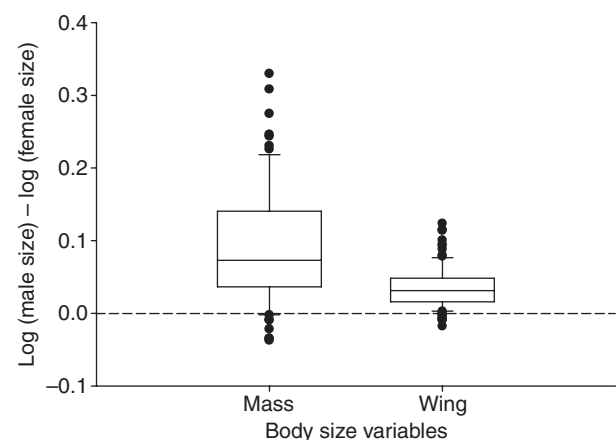

Fig. 2 Boxplot showing the distribution of sexual size dimorphism in body mass (g) and wing length (mm) in Phasianidae. Boxes show inter-quartile ranges and medians are indicated by horizontal lines within each box, whiskers show 10% and 90% percentiles.
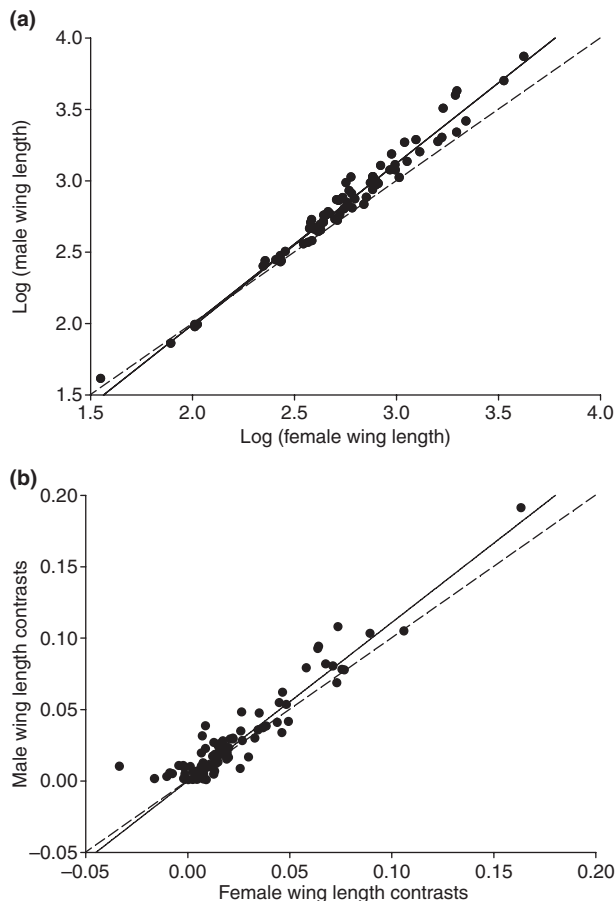
(a)

(b)

Fig. 3 Support for Rensch's rule in Phasianidae. Male-biased sexual size dimorphism in wing length increases with body size (a) using species-level data ($n = 93$) and (b) phylogenetically independent contrasts ($n = 84$ contrasts). The broken line indicates the isometric relationship and the solid line shows the fitted relationship using major-axis regression (through zero for contrasts).

Functional hypotheses of SSD

Sexual size dimorphism increased with the intensity of mating competition in body mass ($\lambda = 1$, $\chi_1^2 = 8.98$, $P = 0.003$, $r = 0.37$), but not in wing length ($\lambda = 1$, $\chi_1^2 = 0.64$, $P = 0.42$, $r = 0.09$). Furthermore, SSD was not related to male display type (body mass: $\lambda = 0.598$, $\chi_1^2 = 2.46$, $P = 0.12$, $r = -0.22$; wing length: $\lambda = 0.642$, $\chi_1^2 = 0.46$, $P = 0.50$, $r = -0.09$). These results largely remained unchanged in multiple regressions with SSD as the dependent variables, both for the body size variable mass (mating competition: $r_{42} = 0.38$, $P = 0.01$; male display type: $r_{42} = -0.16$, $P = 0.31$; full model: $\lambda = 1$, $\chi_3^2 = 9.88$, $P = 0.02$) and wing length (mating competition: $r_{47} = 0.11$, $P = 0.46$; male display type: $r_{47} = -0.07$, $P = 0.63$; full model: $\lambda = 0.84$, $\chi_3^2 = 2.04$, $P = 0.56$).

As predicted by the fecundity hypothesis, female size increased with clutch mass (body mass: $\lambda = 1$, $\chi_1^2 = 56.12$, $P < 0.0001$, $r = 0.80$; wing length: $\lambda = 0.996$, $\chi_1^2 = 40.40$, $P < 0.0001$, $r = 0.72$). However, contrary to the prediction, male-biased SSD increased with clutch mass (body mass: $\lambda = 0.805$, $\chi_1^2 = 5.78$, $P = 0.02$, $r = 0.34$; wing length: $\lambda = 0.849$, $\chi_1^2 = 6.48$, $P = 0.01$, $r = 0.33$). As the latter test could be confounded by the underlying positive correlation between SSD and female body size (Rensch's rule; see above), we repeated the analysis whilst controlling for female body size. The results show that only female body size is significantly correlated with SSD, whereas clutch mass is not, both when using body mass as size variable (female body size: $r_{45} = 0.48$, $P < 0.001$; clutch mass: $r_{45} = -0.24$, $P = 0.11$; full model: $\lambda = 0.854$, $\chi_3^2 = 78.78$, $P < 0.0001$) and using wing length (female body size: $r_{53} = 0.38$, $P = 0.004$; clutch mass: $r_{53} = -0.02$, $P = 0.87$; full model: $\lambda = 0.910$, $\chi_3^2 = 56.92$, $P < 0.0001$).

We found no support for the resource division hypothesis, since neither absolute SSD in body mass ($\lambda = 0.678$, $\chi_1^2 = 2.64$, $P = 0.10$, $r = -0.19$) nor in wing length was related to time when the male and the female shared a territory ($\lambda = 0.720$, $\chi_1^2 = 0.98$, $P = 0.32$, $r = -0.10$).

Directional analyses

Using bivariate categories of SSD, conclusions from analyses on correlated evolution differed widely according to methods (Table 1). The only method that produced significant and fairly consistent results among phylogenies was using midpoints as cut-off points. Here, inferred changes in the intensity of mating competition were positively correlated both with changes in wing length SSD and changes in body mass SSD, although only nonsignificantly so in the latter case ($P = 0.07$). Regardless of phylogeny, and using midponts as cut-off points, evolutionary transitions to male-biased SSD in wing length was more likely in lekking than in nonlekking species. The same relationship appeared when mean values of SSD in body mass were used as cut-off points (Fig. 4; Table 1). Reverse evolutionary transitions in SSD were never related to mating system, nor did mating system evolution depend on levels of SSD ($P > 0.06$ for all comparisons; Fig. 4; Table 1).

Discussion

This study demonstrates that lekking phasianids exhibit more male-biased SSD in body mass than nonlekking ones. This relationship holds when we controlled for potentially confounding variables. Hence, our work strengthens previous findings from more restricted data sets in grouse (Sigurjónsdóttir, 1981; Sæther & Andersen, 1988; Drovetski et al., 2006; Kolm et al., 2007). However, the relationship between SSD and mating system, as well as tests of temporal evolutionary events, depended on the body size variable used. In a comprehensive analysis of

Table 1 Results from likelihood ratio tests (LRT) of (1) correlated evolution (Corr.) between sexual size dimorphism (SSD) and mating systems (LRT statistics are reported), and (2) the temporal sequence of SSD evolution in relation to mating system evolution (alternative transition pathways defined by *q*-values; see Methods and Fig. 4). Mating system is categorized as lek polygyny or not. SSD is calculated as log(male size)–log(female size) and scored as male-biased or not using four different cut-off points calculated by using data from all species. Cut-off points in percent refer to how much larger than females males must be for a species to be classified as sexually size dimorphic. Separate results are given for wing length data and body mass data, and for the two alternative phylogenetic hypotheses in which the genus *Francolinus* is treated as either a monophyletic or polyphyletic group. Significant test results are shown in bold.

	Cut-off point	Corr.	P	q31 = q42 χ^2	P	q12 = q34 χ^2	P	q43 = q21 χ^2	P	q13 = q24 χ^2	P
Wing											
Francolinus polyphyl.	Midpoint	10.660	**0.01**	0.015	0.91	0.094	0.77	0.507	0.48	5.501	**0.02**
	Median	3.976	0.29	1.763	0.19	0.504	0.49	0.935	0.34	1.010	0.32
	Mean	3.422	0.44	1.037	0.31	0.744	0.41	0.983	0.33	0.751	0.40
	5%	4.440	0.30	3.507	0.06	0.185	0.67	1.137	0.29	0.290	0.59
Francolinus monophyl.	Midpoint	10.60	**< 0.01**	0.046	0.84	0.011	0.92	0.487	0.49	5.364	**0.02**
	Median	3.766	0.39	1.590	0.21	0.515	0.48	1.070	0.30	0.908	0.35
	Mean	3.726	0.48	1.087	0.30	0.761	0.40	0.971	0.33	0.796	0.39
	5%	5.220	0.31	3.670	0.06	0.180	0.67	1.025	0.31	0.308	0.58
Body mass											
Francolinus polyphyl.	Midpoint	5.944	0.07	1.155	0.29	1.091	0.30	0.201	0.67	0.118	0.74
	Median	3.672	0.40	0.628	0.44	0.157	0.70	1.605	0.21	0.655	0.44
	Mean	9.062	**< 0.01**	1.821	0.18	0.862	0.37	2.015	0.17	5.335	**0.02**
	10%	10.47	**< 0.01**	0.304	0.58	0.242	0.62	1.292	0.26	0.252	0.62
Francolinus monophyl.	Midpoint	5.546	0.07	0.922	0.35	1.054	0.31	0.124	0.73	0.031	0.87
	Median	3.624	0.40	0.551	0.47	0.350	0.57	2.346	0.13	0.571	0.46
	Mean	8.000	0.09	1.720	0.19	0.630	0.44	2.081	0.16	4.049	**0.05**
	10%	10.613	**0.02**	0.569	0.45	0.054	0.82	1.489	0.22	0.140	0.71

SSD in birds (Székely *et al.*, 2007), we have shown that different measures of SSD are only weakly correlated. One reason for qualitative differences between tests
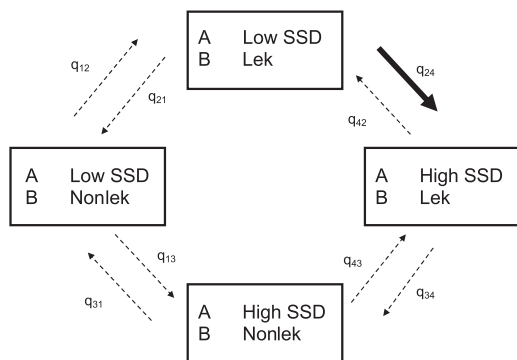

Fig. 4 Flow diagram showing the eight possible transition rate parameters in the co-evolution of (a) sexual size dimorphism (SSD) in wing length and (b) lek polygyny. Directionality of evolutionary transitions is tested by forcing related transition parameters to take the same values. This represents the null hypothesis, i.e. that transitions are equally likely. Significant models show a reduced fit to the data, suggesting that one transition parameter is more probable than the other. Here, the solid arrow indicates that the evolutionary transition from low to high SSD is more likely in lekking species than in nonlekking species ($P = 0.02$) and therefore that the null hypothesis (q13 = q24) could be rejected.

based on body size and linear measurements may be that body mass is a three-dimensional measure, possibly amplifying SSD in a single-dimensional trait. Moreover, different morphological traits may be subject to different selection pressures (Björklund, 1990). Analyses of SSD variation should therefore preferably be performed on more than one measure of body size to get a complete picture of the selective forces operating on bird morphology, and ultimately leading to SSD.

The sexual selection hypothesis of SSD evolution predicts that male mating success should increase with body size. However, field studies failed to demonstrate this expected relationship within species (Gibson & Bradbury, 1985; Höglund & Alatalo, 1995; Rintamäki *et al.*, 2001; but see Brodsky, 1988). Hence, in cases where sexual selection in lekking species resulted in the evolution of SSD in the past, the respective selective forces may not necessarily be working today. Instead, female choice and male dominance hierarchies may be determined by a suite of characters not only involving male body size but also other morphological variables such as comb size (Bart & Earnst, 1999; Redpath *et al.*, 2006; Siitari *et al.*, 2007), and/or behavioural traits like display intensity (Gibson & Bradbury, 1985; Chappell *et al.*, 1997). Also, despite the lack of support in the present study, we cannot entirely rule out that other selective forces than sexual selection may contribute to SSD evolution. For example, in our experience mating

systems are better described and are therefore more readily categorized than display agility and inter-sexual niche segregation. Hence, our analyses of the latter hypotheses may suffer from poorer data quality than mating system.

Analyses testing if lek behaviour evolved prior to SSD in body mass are not robust but depend on the methods used for bi-variate classification of SSD. Nevertheless, the only significant relationship was the one expected from the sexual selection hypothesis, namely that lek behaviour evolved prior to SSD. That none of our directional analyses supported the notion that SSD evolved prior to lekking contradict previous findings from a restricted analysis on grouse species (Höglund, 1989; see also Oakes, 1992; Höglund & Sillén-Tullberg, 1994). A possible reason for this is that we used statistical tests to investigate the relationship whereas Höglund (1989) performed a less objective inspection of the phylogeny. Further, phylogenetic hypotheses advanced rapidly in recent years because of an abundance of DNA sequence data. Better phylogenies and more data can have fundamental influences on the results of comparative analyses (Lecointre *et al.*, 1993). On a more general basis it is also important to note that, when continuous variables are used in directional analyses, focusing on a single cut-off point may lead to misleading conclusions.

We failed to find support for the display agility hypothesis. However, sexual selection for larger males cannot be the only evolutionary force shaping SSD in lekking birds, as the body size of males is equal to, or smaller than, that of females in many such species. A possible reason for lacking male-biased SSD in lekking species may be that traits other than body size are targeted by sexual selection, such as song repertoires and plumage showiness (Höglund, 1989). In a comprehensive study of SSD in birds, we found support for the display agility hypothesis across over 3500 species (Székely *et al.*, 2007). However, within the Phasianidae, no species show agile flight displays like those described from specific bird groups where such behaviour is known to influence the evolution of male body size (Figuerola, 1999; Székely *et al.*, 2004; Raihani *et al.*, 2006; Serrano-Meneses & Székely, 2006). Thus, it is possible that selection for flight agility may only explain SSD in species in which display consists of extreme flight acrobatics. Interestingly, the relationship between sexual display characteristics and SSD has already been demonstrated in two other families with a lekking mating system (shorebirds, Székely *et al.*, 2000; and bustards, Raihani *et al.*, 2006), and the interaction between intensity of mating competition and male display agility may explain the failure of previous analyses to identify the relationship between lekking and size dimorphism.

As predicted by the fecundity hypothesis large females laid heavier clutches. Yet, we failed to find the predicted negative correlation between clutch mass and male-biased SSD when controlling for female body size. The reason for this could be that even if fecundity advantages do select for larger females, the benefits of being large in males exerts even stronger selection pressure. Moreover, we were unable to include the number of clutches laid per season in our analyses because such data are lacking for most species. Consequently, the resulting fecundity indexes may be too imprecise (Kolm *et al.*, 2007). Extending this reasoning, Shine (1988) noted that selection should act on the total life-time reproduction, not reproductive success (and thus clutch and egg sizes) within single breeding events. The best female strategy, i.e. large body and heavy clutches vs. small body and lighter clutches, may depend on the trade-off between growth and reproduction. If energy and nutrients are limited large females must have used more of these resources on growth than on reproduction early in life. Consequently, fecundity selection may only apply to egg-producing species which are not energy limited, and this may not be the case in Phasianid species. A recent study on Galliform genera (i.e. including the Phasianidae; Kolm *et al.*, 2007) showed that egg size and female size, but not clutch size, related positively to SSD, and directional analyses suggested that the evolution of increased SSD subsequently led to increases in female size, and correlated changes in egg size. Hence, SSD may affect the evolution of avian egg sizes and clutch masses, if not the other way around (see also Cabana *et al.*, 1982; Weatherhead & Teather, 1994).

In conclusion, our results are most consistent with the proposition that lekking behaviour promoted male-biased SSD in grouse and allies. Although our directional analyses were not robust but depended on how SSD was categorized, the only significant relationship supported the hypothesis that lekking evolved before SSD. We have also shown that although clutch mass is positively correlated with female body size, it is not related to SSD. Nor did we find support for the resource division hypothesis. Given our results using the largest dataset for grouse and allies as yet, we suggest the relationship between lek behaviour and SSD should be re-evaluated in birds by considering interspecific differences in sexual display characteristics, a factor that is often associated with reduced male size even in polygynous species.

Acknowledgments

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Appendix 1

Data from the Phasianidae which are used to calculate sexual size dimorphism (SSD), together with variables of fecundity, mating competition and resource division. Columns show (1) male body mass (g), (2) female body mass (g), (3) male wing length (mm), (4) female wing length (mm), (5) clutch size, (6) egg mass (g), (7) mating system (1, nonlekking; 2, lekking), (8) sexual display agility (1, ground display, including display on trees and on bushes; 2, ground display, but with occasional leaps and jumps into the air; 3, both ground and aerial displays including jumps), (9) sexual resource division (1, males and females do not share resources, and feed away from their breeding site; 2, males and females share resources on their territory only during the breeding season; 3, males and females share resources on their territory all year round), (10) body mass SSD (0, below average; 1, above average) and (11) wing length SSD (0, below average; 1, above average).

Species name	1	2	3	4	5	6	7	8	9	10	11	References
Afropavo congensis	–	–	318	286	3.09	70	1	1	1.75	–	1	5, 7, 9, 11
Alectoris barbara	461	376	166	156	12	19.6	1	2	1	0	0	1, 6, 7, 9, 11
Alectoris chukar	536	501	168	154	15.5	22.5	1	1	0.5	0	1	1, 9, 10
Alectoris graeca	700	575	171	162	11.5	19.7	1	1	1	0	0	1, 2, 4, 6, 7
Alectoris magna	577.5	528.5	174.5	166	–	20.4	–	–	–	0	0	6, 7
Alectoris melanocephala	724	522	193.5	173.5	6.5	–	–	–	0	1	1	6, 7
Alectoris rufa	516	439	165	157	12.7	20.1	1	1	1	0	0	1, 2, 6, 7, 9
Argusianus argus	–	–	–	–	2	74.3	1	1	0.5	–	–	5, 7
Bambusicola thoracica	269.5	271	132	129.5	5	11.9	–	–	1	0	0	6, 7
Bonasa bonasia	369	370	168	165	9.38	19	1	2	0.75	0	0	1, 7, 9
Bonasa sewerzowi	278	257	176	141.5	6.5	–	1	2	–	0	1	4, 5, 7, 9
Bonasa umbellus	585	472	182.4	176	11.5	18	2	1	0.25	1	0	2, 4, 7, 9, 10
Catreus wallichii	1587.5	1305	252.5	235	10.5	71.6	1	1	1	0	0	5, 7
Centrocercus urophasianus	3200	1700	340	284	7.26	46.1	2	1	0.5	1	1	4, 7, 10
Chrysolophus amherstiae	762.5	714	220.5	198.5	9	31.1	1	1	1	0	1	1, 5, 7
Chrysolophus pictus	642.5	607.5	195	187	9	26.7	1	1	1.75	0	0	1, 5, 7, 9
Coturnix chinensis	41	35.6	72.1	72.2	7.5	4.8	1	1	1.75	0	0	2, 6, 7, 8, 9
Coturnix coturnix	94.5	103	111	113	10.3	8.2	1	1	1	0	0	1, 2, 6, 7, 9
Coturnix delegorguei	72.4	78.5	96	100	4.8	7.5	1	2	0.75	0	0	6, 7, 9, 11
Coturnix pectoralis	97.9	106	102.1	104.3	10.5	8.6	1	–	1.5	0	0	2, 6, 7, 8, 9
Coturnix ypsilophora	98	103	98.3	100.3	7.9	11.2	1	1	1.5	0	0	2, 6, 7, 8, 9
Crossoptilon auritum	1875	1600	299.5	297	6.5	63	1	1	1	0	0	5, 7
Crossoptilon crossoptilon	2000	1675	318	290	7.4	53.24	1	1	1	0	1	5, 7
Dendragapus canadensis	492	424	182	180.5	6	22.8	2	3	0.75	0	0	2, 7, 10
Dendragapus falcipennis	680	695	192.5	185	11.5	26	–	2	1	0	0	4, 7
Dendragapus obscurus	1273	839	229	208	8.5	32.5	2	3	0.5	1	1	2, 7, 9, 10
Francolinus adspersus	461	394	177	163	6.7	26.8	1	1	1.5	0	1	6, 7, 9, 11
Francolinus afer	–	–	192	182	5.5	33	1	1	1.75	–	0	6, 7, 9, 11
Francolinus africanus	456	397.5	157	153	7.2	17.8	1	–	1	0	0	6, 7, 9, 11
Francolinus ahantensis	–	–	172	164	–	25.2	1	–	1.5	–	0	6, 7, 11
Francolinus albogularis	273.5	273.5	135	127	5.5	14	1	–	1	0	0	6, 7, 9, 11
Francolinus bicalcaratus	507	381	177.5	169	5.5	26.5	–	–	1	1	0	1, 6, 7, 9, 11
Francolinus capensis	757.5	547	212	196	7.4	33	1	–	1.5	1	0	6, 7, 9, 11
Francolinus castaneicollis	1057.5	600	210	186	5.5	37.5	1	–	1.5	1	1	6, 7, 11
Francolinus clappertoni	604	463	180	166	–	23	1	–	1.5	1	0	6, 7, 9, 11
Francolinus coqui	–	–	134	131	5	16.1	1	–	2	–	0	6, 7, 9, 11
Francolinus erckelii	–	–	216	185	7	33	1	–	2	–	1	6, 7, 9, 11
Francolinus finschi	–	–	167	166	–	–	–	–	1	–	0	6, 7, 11
Francolinus francolinus	487.5	425	177	167	5.5	23.5	1	2	1	0	0	1, 6, 7, 9, 10
Francolinus griseostriatus	–	–	153	148	–	–	1		1	–	0	6, 7, 11
Francolinus harwoodi	–	–	–	–	–	–	–	–	1.5	–	–	6, 7, 11
Francolinus hildebrandti	–	–	174	162	6	26.3	1	–	1.5	–	0	6, 7, 9, 11
Francolinus icterorhynchus	571	441	169	157	7	19.9	–	–	1.75	1	0	6, 7, 9, 11
Francolinus jacksoni	–	–	218	200	–	32.9	1	–	2	–	1	6, 7, 11
Francolinus leucoscepus	753	545	200	187	–	30.8	1	1	1.75	1	0	6, 7, 9, 11
Francolinus levaillantii	463	401	162	158	5	21	1	–	1	0	0	6, 7, 9, 11
Francolinus levaillantoides	454	414.5	163	160	6	18.75	1	–	1	0	0	6, 7, 11
Francolinus natalensis	532.5	385	168	156	6.5	27	1	–	1.5	1	0	6, 7, 11

Appendix 1 (*Continued*).

Species name	1	2	3	4	5	6	7	8	9	10	11	References
Francolinus nobilis	–	–	198	178	–	–	–	–	1.5	–	1	6, 7, 11
Francolinus ochropectus	809	605	–	–	–	–	–	–	1	1	–	6, 7, 11
Francolinus pondicerianus	274	228	153	140	7.5	12.7	–	–	1	0	1	6, 7
Francolinus rufopictus	848	588	213	190	–	28.4	1	–	1.5	1	1	6, 7, 9, 11
Francolinus schlegelii	251	223	128	123	–	10.5	1	–	1	0	0	6, 7, 11
Francolinus shelleyi	450	426	162	157	4.8	17.3	1	–	1	0	0	6, 7, 11
Francolinus squamatus	510	440	175	163	–	21.7	1	–	2	0	0	6, 7, 11
Francolinus streptophorus	–	–	150	152	–	–	1	–	1	–	0	6, 7, 11
Francolinus swainsonii	732	510	191	174	5.5	29.1	1	–	1.5	1	1	6, 7, 9, 11
Gallus gallus	1061	767.5	226.5	188.5	6	29.6	1	1	1.25	1	1	2, 5, 7, 8
Gallus lafayetii	965	567.5	228	175	3	30.4	1	1	1	1	1	5, 7
Gallus sonneratii	963	747.5	237.5	207.5	4.5	33.4	1	1	1.5	1	1	5, 7
Gallus varius	1061	767.5	232.5	187.5	3.5	29.2	1	1	1	1	1	5, 7
Ithaginis cruentus	525	515	–	–	8.5	28.8	1	1	2	0	–	5
Lagopus lagopus	635	555	208	195	9.5	21.5	1	3	1	0	0	1, 2, 4, 5, 7, 9, 10
Lagopus leucurus	359	351	200.5	193.2	5.9	20	1	1	1	0	0	2, 4, 7, 9, 10
Lagopus mutus	439	414	203	189	8.5	20	1	3	1	0	0	1, 2, 7, 9
Lophophorus impejanus	2180	1975	304.5	273	6	70.7	1	3	1	0	1	5
Lophophorus lhuysii	–	–	–	–	–	99.4	–	1	1	–	–	5
Lophophorus sclateri	2607.5	2196.5	300.5	286	–	70.5	–	–	0.5	0	0	5
Lophura edwardsi	–	–	230	215	5.5	32.2	–	1	0	–	0	5, 7
Lophura leucomelanos	995	794	252.5	216.5	7.5	37.4	1	1	1.5	1	1	2, 5, 7
Lophura nycthemera	1360	1130	272.5	248.5	5	42.8	1	1	1.25	0	1	5, 7, 9
Lophura swinhoii	–	–	255	242.5	5.5	40.6	–	1	1	–	0	5, 7
Margaroperdix madagarensis	–	–	125	126	17.5	–	–	–	1.5	–	0	6, 7
Meleagris gallopavo	7400	4222	511	417	12.5	78.8	2	1	0	1	1	2, 4, 7, 9, 10
Pavo cristatus	5000	3375	470	410	6	103.5	1	1	0.25	1	1	5, 7
Pavo muticus	–	–	480	435	4.5	114.9	1	1	0.75	–	1	5, 7
Perdix dauurica	297	270	139	139	18	12.7	–	–	1	0	0	6, 7
Perdix perdix	378	386	159	154	14.6	14.5	1	1	1.5	0	0	6, 7
Phasianus colchicus	1186	989	245	215	11	31.5	1	2	0.5	0	1	1, 2, 5, 7, 9
Polyplectron bicalcaratum	–	–	225	195	2	37.3	1	1	1.75	–	1	5, 7
Polyplectron chalcurum	–	–	176	156	2	35	–	1	1.5	–	1	5, 7
Polyplectron emphanum	–	–	192.5	172.5	2	32.2	1	1	1.75	–	1	5, 7
Polyplectron germaini	–	–	190	172.5	2	30.4	–	1	1.5	–	1	5, 7
Polyplectron inopinatum	–	–	242.5	182.5	2	40.2	–	1	2	–	1	5, 7
Polyplectron malacense	–	–	207.5	182.5	1	40.5	–	1	0.25	–	1	5, 7
Pucrasia macrolopha	1184	932	212.4	196.7	6	40	1	1	2	1	0	5
Rheinardia ocellata	–	–	375	335	2	75.3	–	2	0.5	–	1	5, 7
Syrmaticus reevesii	1529	949	287.5	242.5	9.5	34.8	–	1	1	1	1	5, 7
Tetrao mlokosiewiczi	865	766	206	200	6.1	32.5	2	2	0.25	0	0	1, 7, 9
Tetrao parvirostris	3965	1950	392	311	6.5	54	2	2	0	1	1	4, 7
Tetrao tetrix	1290	988	257	226	7.91	35.5	2	2	0.25	1	1	1, 7, 9
Tetrao urogallus	4240	1985	390	300	6.2	53	2	3	0.25	1	1	1, 2, 7, 9
Tragopan blythii	1930	1250	262.5	237.5	3.1	62	–	1	2	1	1	5
Tragopan caboti	–	–	217.5	207	3	44.2	1	1	1.5	–	0	5
Tragopan satyra	1850	1100	268.5	229.5	3	63.3	1	1	1	1	1	5
Tragopan temminckii	1050	1035	245	222.5	4	47.7	1	1	1	0	1	5
Tympanuchus cupido	933	795	229	226	12	24.5	2	2	0	0	0	2, 4, 7, 9, 10
Tympanuchus pallidicinctus	743	628	210.4	202.8	10.7	24	2	2	0	0	0	4, 7, 9, 10
Tympanuchus phasianellus	953	817	–	–	10.9	24	2	2	0.25	0	–	2, 4, 7, 10

References: (1) Cramp & Simmons (1980)); (2) Dunn *et al.* (2001); (3) Fry & Keith (2000); (4) Johnsgard (1983); (5) Johnsgard (1986); (6) Johnsgard (1988); (7) Madge & McGowan (2002); (8) Marchant & Higgins (1993); (9) Schönwetter (1967); (10) Poole, 2005); (11) Urban *et al.*, 1986;.

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